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A SEASONAL AND ECOLOGICAL SURVEY OF FRESHWATER LIMPET SNAILS (PULMONATA: ANCYLIDAE) AND THEIR DIGENETIC TREMATODE PARASITES IN SOUTHEASTERN LOUISIANA

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ABSTRACT

An 18-month survey involving almost 20,000 freshwater limpet snails of the family Ancylidae revealed three species, each representing a different genus, occurring in southeastern Louisiana.

Laevapex fuscus was collected only from lentic habitats, where it exhibited, at most, a bivoltine pattern of reproduction with two successive generations per year; in habitats of low primary productivity a single annual generation was produced. *Ferrissia fragilis* was collected from lotic and lentic habitats and produced a single annual generation. *Hebetancylus excentricus* also displayed a broad habitat preference but exhibited up to a trivoltine pattern of reproduction.

Southeastern Louisiana ancylid snails play a major role in the ecology of digenetic trematodes since 19 species of larval trematodes were found developing in three ancylid species. Hosts, descriptions, seasonal incidence, and possible identity of these cercariae are given.

Seasonal occurrence of trematode intramolluscan stages was closely related to seasonal occurrence of the ancylid snail hosts. Bivoltine patterns of reproduction for *Hebetancylus excentricus* were reflected in two generations of cercarial production.

On the basis of comparative ecology, anatomy, and hosted trematodes, we propose that *Hebetancylus* occupies an intermediate phylogenetic position between *Ferrisia* and *Laevapex*. *Ferrissia* is least specialized in terms of its hosted trematode fauna, which bears similarity to that hosted by snails of the family Planorbidae.

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INTRODUCTION

Literature on parasites of ancylid snails is meager, with less being known than for other major families of freshwater gastropods (Malek and Cheng, 1974). Smith (1967) reviewed the literature on larval digenetic trematodes developing in ancylids and noted that the six reports from 1827 to 1959 were incomplete in description, with no indication as to specific or generic identity of the adult trematodes. None was from North America.

Smith (1959) was the first to report North American ancylid snails as first intermediate hosts for trematodes. He reported the occurrence of *Megalodiscus temperatus* (Stafford, 1905) in *Ferrissia fragilis* (Tryon, 1863) in Michigan. The life cycle of this rectal parasite of frogs had been elucidated by Krull and Price (1932), who implicated the planorbid snail *Helisoma trivolvis* (Say, 1817) as a natural snail host.

Peters and Self (1963) reported an ophthalmoxiphidiocercaria of the family Allocreadiidae Stossich, 1903 developing in *Laevapex fuscus* (C.B. Adams, 1841) from southeastern Oklahoma and encysting in the mantle of unionid clams and limpets, including limpets hosting the rediae. These investigators believed the cercaria to be that of *Allocreadium ictaluri*

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Pearse, 1924, an intestinal parasite of catfish. They noted that miracidia, hatched from eggs obtained from infected catfish, penetrated and remained in the tissues of *L. fuscus*. All other members of the trematode family Allocreadiidae, for which life cycles are known, utilize sphaeriid clams as first intermediate hosts (Yamaguti, 1975).

Basch (1963), in his monograph on North American Ancylidae, noted that of 150 ancylid collections taken during the summer of 1961, from 23 states, about 15% were heavily infected with one or more species of trematode larvae.

Smith (1967) examined *Ferrissia fragilis, F. parallela* (Haldeman, 1841), and *Laevapex fuscus* from several marsh pond, stream, and river localities in southeastern Michigan. Fifteen different trematode species were found to use one or more of the three limpet species as first intermediate hosts. Unfortunately, Smith did not figure or otherwise describe those cercariae except to note that *Megalodiscus temperatus* developed in all three limpet species. Identification of the other 14 cercariae was only to the level of superfamily or family.

In addition to *Megalodiscus temperatus*, Smith (1967) noted another amphistome developing in *Ferrissia parallela*; a strigeoid in *F. fragilis*; another in *F. parallela*; an echinostomatid in *F. fragilis*; two others in *F. parallela*; a fourth in *Laevapex fuscus*; a spirorchiid in *F. fragilis, F. parallela*, and *L. fuscus*; a lissorchiid and cyanthocotylid in *L. fuscus*; and three xiphidiocercariae in *F. parallela*. Significance of the apparent specificity exhibited by most cercariae is tempered by Smith's failure to note the occurrence of sympatry among the limpet hosts.

Smith (1968) reported that lissorchiid cercariaea (tailless cercariae), previously reported (Smith, 1967) in *Laevapex fuscus* from Michigan, also parasitized *Ferrissia rivularis* (Say, 1817) in southeastern Michigan. According to Smith, this cercariaeum was identical to *Cercariaeum mutabile* described by Cort (1918) and reported by Wallace (1941) to be the larva of *Triganodistomum mutabile* (Cort, 1918), an intestinal parasite of catostomid fishes. Wallace (1941) reported *Helisoma trivolvis* and *H. campanulata* (Say, 1821) as natural snail hosts, with the planarian *Dugesia* sp. or the commensal annelid, *Chaetogaster limnaei* von Baer, 1827 serving as second intermediate host for *T. mutabile*.

Duncan and DeGiusti (1976) produced evidence that the lisorchiid cercariaeum, thought by Smith (1968) to be *Cercariaeum mutabile*, was in fact a complex of three cercarial species. These cercariaea differed in size, arrangement of tegumental papillae, tegumental spination patterns, and species of intermediate hosts. Since Duncan and DeGiusti believed them to be larval stages of described lissorchiids, they did not formally describe them as new species. They did, however, provide full descriptions while designating them as *Cercariaeum* types I through III. *Cercariaeum* type I utilized *Laevapex fuscus* as first intermediate host with *Chaetogaster limnaei* as second intermediate. *Cercariaeum* types II and III utilized *L. fuscus* and *Ferrissia rivularis* respectively, while *Chaetogaster limnaei, Dugesia tigrina* (Girard, 1850) and *D. dorotocephala* (Woodworth, 1897) served as second intermediates.

Underwood and Dronen (1977) reported an unidentified species of *Ferrissia* from Texas as an experimental host for the frog lung fluke *Haematoloechus breviplexus* Stafford, 1902. These investigators noted that xiphidiocercariae obtained from *Ferrissia* sp. were smaller at maturity than *H. breviplexus* cercariae described by Schell (1965) from the experimentally infected planorbid snail *Gyraulus similaris* (F.C. Baker, 1919).

Turner and Corkum (1977) reported *Ferrissia fragilis* as a natural snail host for the turtle blood fluke *Spirorchis scripta* Stunkard, 1923 in Louisiana. The larva of *S. scripta* had previously been reported to develop in certain species of naturally infected planorbid snails (Goodchild and Kirk, 1960; Holliman and Fisher, 1968). From the above review, ancylids obviously appear to have been a neglected group in most parasitological studies.

The objectives of this study were as follows: (1) to survey the freshwater limpet (Ancylidae) fauna of southeastern Louisiana, (2) to investigate related ecological aspects including habitat, seasonality, and population dynamics, (3) to investigate its role in the ecology of digenetic trematode parasites, (4) to provide descriptions and figures of those trematode cercariae developing in southeastern Louisiana ancylids, (5) to identify cercariae by life cycle studies and/or a survey of trematode life history literature, and (6) to postulate a phylogenetic relationship for southeastern Louisiana ancylids based upon similarities and differences in hosted trematodes.

MATERIALS AND METHODS

Limpets were collected biweekly, for up to 18 consecutive months, from five ecologically dissimilar localities in southeastern Louisiana. Collecting sites, with survey period in parentheses, were as follows: drainage ditch on Ben Hur Road Experimental Farm, 1 mi S of LSU Baton Rouge campus, East Baton Rouge Parish, (June 1975-November 1976); Beaver Pond Branch, 3 mi SE of Livingston, Livingston Parish. on Interstate Highway 12 (July 1975-November 1976); borrow pit on W side of Atchafalaya floodway levee at Ramah, Iberville Parish, on Interstate Highway 10 (July 1975-August 1976); roadside swamp, 2 mi SE of Sorrento, Ascension Parish, on Rt. 61 (June 1975-July 1976); and pond, 2 mi E of Head of Island, Livingston Parish, on Rt. 22 (June 1975-August 1976).

Collections were made by removing, with a sharp scalpel blade, limpets attached to submerged or floating debris as well as leaves and stems of floating or submerged vegetation. Specimens were placed in glass finger bowls containing water from the collecting site. Bowls rested on an inverted styrofoam ice chest that served as a floating work table.

Collecting time for each of the 156 collections was a multiple of 15 minutes duration. This was done to establish an index of relative abundance by noting number of limpets collected during 15 minutes. To roughly determine population structure, all individuals seen, regardless of size, were collected.

Snails were maintained in their collection containers until identified, graded into sizes, and examined for larval digenetic trematodes; this was usually done within 24 hours after collection. Voucher specimens of all limpet species were deposited in the mollusc collection of the Delaware Museum of Natural History (DMNH).

The smaller limpet species *Ferrissia fragilis* (DMNH 119530) was graded into three size classes based upon shell length: <2 mm, 2-4 mm, and>4 mm. *Laevapex fuscus* (DMNH 119532) and *Hebetancylus excentricus* (Morelet, 1851) (DMNH 119531) were graded into classes:<3 mm, 3-5 mm, and>5 mm. Presumably changes, over the course of our survey, in relative numbers of each class should reflect population dynamics, including reproduction, recruitment, and death. Although collections were biweekly, data on limpet populations were pooled for each month.

Visual screening for digenetic trematode larvae was possible since most of the limpet's "soft-parts," including the digestive gland, were exposed to inspection when the snail was inverted. Identification was made by dissection or by allowing cercariae to emerge from live, isolated individuals. Limpets without visible germinal sacs (rediae or sporocysts) were dissected and examined for immature larval stages and/or metacercariae.

Biweekly data on incidence of infection, like those used for population biology, were pooled for each month. Only those individuals of *Hebetancylus excentricus* and *Laevapex fuscus* greater than 3 mm shell length were considered when computing monthly incidence. Neither cercariae or germinal sacs were evident among the smaller individuals; however, this was not true for *Ferrissia fragilis*, all sizes of which were considered when computing incidence.

Cercariae, designated as types I-XIX (Figures 1-19) were studied live and unstained, vitally stained with nile blue, or fixed in hot 10% formalin. Unless otherwise noted, measurements were taken from 10-20 formalin preserved specimens under light coverslip pressure and are expressed in microns. Ranges are given with mean in parentheses. Drawings are composites made from live and preserved specimens, either free hand, with aid of a microprojector, or from photomicrographs.

RESULTS AND OBSERVATIONS

Ecology of Southeastern Louisiana Ancylids

After 18 months of collecting and examining almost 20,000 ancylid specimens, three species, each representing a different genus, were found to occur in our study areas. *Laevapex fuscus* was collected from submersed stems of emergent vegetation and from submersed debris at three localities exhibiting a lentic character. *Ferrissia fragilis* and *Hebetancylus excentricus* occurred on emergent and floating vegetation at all five collecting sites, which along with the seasonality and population dynamics of their ancylid snail faunas, are characterized below.

1. Ben Hur Experimental Farm (BHF)

This 3 m wide, mud-bottom ditch, although never dry, had an intermittent flow and drained the LSU experimental farm and 20 shallow ponds for experimental rearing of catfish and crayfish. During the 18-month survey of this locality, 3,774 *Hebetancylus excentricus* and 172 *Ferrissia fragilis* were collected exclusively off submersed leaves and stems of alligator weed (*Alternanthera* sp.). *Laevapex fuscus* was not seen or collected.

Population dynamics and seasonal abundance of both *Ferrissia fragilis* and *Hebetancylus excentricus* are presented in Figure 20. *F. fragilis* was collected intermittently and in small numbers during the course of the survey at BHF. Usually fewer than two individuals were collected per 15 minutes of collecting effort. A peak in numbers occurred in April, when about 10 limpets were collected per 15 minutes. This peak was followed by a gradual decline to zero in August. Recruitment occurred in mid spring as evident by the increasingly greater percentage of the population comprised by individuals of the small size class (<2 mm length). Individuals of the large size class (>4 mm length), probably representing the post-ovigerous segment of the population, were collected only at this time. Basch's (1963) observation of maximum length of 4 mm for *F. fragilis* may substantiate a post-ovigerous role for those large size class individuals. However, large size class (>5 mm length) *Laevapex fuscus* and *H. excentricus*, noted by Basch to have maximum lengths of 7.75 and 5.8 mm respectively, would not necessarily comprise the post-ovigerous segment.

Hebetancylus excentricus was present throughout the study and exhibited two distinct population peaks: one in November, and another in May. This species displayed a bivoltine pattern of reproduction with two successive generations per year as evident by the observation that peaks in the index of relative abundance coincide with or closely follow periods of increase in percentage of small size class individuals (< 3 mm length). In *H. excentricus*, reproduction and recruitment are preceded by a build up in percentage of the large size class sector of the population.

2. Beaver Pond Branch (BPB)

This narrow, continuously flowing stream originates near Livingston, Louisiana, and empties into Hog Branch, a larger, sand-bottomed stream forming part of the drainage for the so-called Florida Parishes of southeastern Louisiana. During periods of high water in Hog Branch (two occurred during our survey) BPB received backwater from Hog Branch. This condition persisted for several days before normal flow returned in both streams.

Hebetancylus excentricus and *Ferrissia fragilis* were collected from floating vegetation and from emergent arrowhead (*Sagittaria* sp.). *Laevapex fuscus* was not encountered. Figure 21 shows population biology and seasonal abundance of 1,294 *H. excentricus* and 1,853 *F. fragilis* collected during 17 months. Seasonality is evident and perhaps reflects seasonal partitioning of the habitat by the two limpet species. From January to July, 1976, *F. fragilis* was present in large numbers at a time when *H. excentricus* was almost absent from the habitat. *H. excentricus* became the predominant limpet species during the fall.

3. Ramah (RAM)

This site is a borrow pit of the Atchafalaya River Basin and is subjected to large fluctuations in water level. Because of fluctuations, emergent vegetation that consisted mainly of *Sagittaria* was seasonal, and occurred mostly in summer and fall. Although no measurement of dissolved oxygen was taken during the study, this habitat would be classified as mesotrophic.

All three limpet species were sympatric at RAM. *Laevapex fuscus* was collected from submersed and floating debris, water hyacinth (*Eichornia crassipes*), and emergent *Sagittaria*. *Ferrissia fragilis* and *Hebetancylus excentricus* were similarly collected; however, *H. excentricus* was seldom found on debris. Limpet population biology and seasonal abundance for 3,663 *L. fuscus*, 577 *F. fragilis*, and 425 *H. excentricus* collected during our 14-month survey are presented in Figure 22.

As at BPB, *Hebetancylus excentricus* and *Ferrissia fragilis* displayed a pronounced seasonality that was interpreted as seasonal partitioning of the habitat. However, seasonality of limpets may also reflect seasonal absence of vegetation on which *H. excentricus* was most often collected. *F. fragilis*, like the BPB population, was abundant in early spring through summer, while *H. excentricus* was most abundant during the fall. Data indicate production of a single *H. excentricus* and *F. fragilis* generation per year.

Laevapex fuscus was the predominant limpet species at RAM and was collected in relatively high numbers almost year round. The low fall-winter index of relative abundance may have been due to *L. fuscus* burrowing into the mud, where they were unavailable for collection by our methods. Indications are that a single generation is produced annually. Recruitment certainly began in April, because population structure for that month demonstrates an expanding population.

4. Sorrento (SOR)

This is a shallow, former, roadside swamp, with a mud bottom. Water level was maintained at about 0.5 m during the first 12 months of the survey; however, in June 1976 the level began to drop and the site was completely dry by August 1976. The 100 m X 30 m area had been cleared several years earlier as right of way for an underground pipeline, and was free of trees. As a result, a luxuriant growth of emergent grass (*Paspalum* sp.) was maintained almost year round and gave the locality a marsh appearance. This site, with its shallowness, abundant emergent vegetation, and high primary productivity, fits the criteria of a eutrophic habitat.

All three ancylid species occurred at this locality; however, as seen in Figure 23 the scale for relative abundance of *Laevapex fuscus* is 10 fold greater than for *Hebetancylus excentricus* and 100 fold greater than for *Ferrissia fragilis*. Total numbers collected were 4,960, 352, and 40, respectively.

Ferrissia fragilis was collected in too small numbers for any determination of population dynamics; however, a pronounced seasonality was noted. *Hebetancylus excentricus* appears to have a single generation each year with recruitment in the spring.

Laevapex fuscus produced a fall and spring generation. Egg hatching and recruitment from one biannual cycle extended into the next, and thus gave the appearance of year-round reproduction. Another observation concerning the *L.*

fuscus population was the predominance of large-size class individuals in most pooled monthly samples. Predominance of large individuals indicates a rapid growth rate, probably attributable to the eutrophic environment, and is striking when compared to the pooled monthly population structures at the less eutrophic Ramah (Figure 22). As will be shown later, apparent differences in productivity have considerable implications for the ecology of the respective digenetic trematode populations.

5. Head of Island Pond (HIP)

This permanent pond has a shallow margin at its north end lined with emergent vegetation. The remaining margin was deep and without emergent vegetation. Much sunken debris – sheets of plastic, metal cans, glass, etc., was found along the front or south margin. *Laevapex fuscus* occurred on this debris; however, because of depth, collecting was difficult. For this reason, *L. fuscus* was not included among the ancylids studied at this locality. We mention the occurrence because it demonstrates habitat selection by the three ancylid species, since *L. fuscus* was found only on this deep water debris, while *Hebetancylus excentricus* and *Ferrissia fragilis* occurred only on debris and emergent vegetation along the shallow margin.

Population biology and seasonal abundance for 1,836 *Hebetancylus excentricus* and 182 *Ferrissia fragilis* collected during our 15-month survey are shown in Figure 24. *F. fragilis* was abundant only in February and March. We believe that presence of individuals classed as large, accompanied by an increasing percentage of the smaller class, indicates recruitment at this time.

Hebetancylus excentricus occurred year round with production of three generations; one in the summer, another in the fall, and the third in the spring.

Digenetic Trematodes in Southeastern Louisiana Ancylids

Cercariae representing 19 trematode species were found developing in one or more of three ancylid species. Hosts, descriptions, seasonality of incidence, and possible identity of these larvae are given below (Figures 20-24).

Cercaria Type I (Figures 1, 21, 22, and 23)

Laevapex fuscus collected from SOR, *Ferrissia fragilis* from BPB, and both species from RAM were found to harbor infections with xiphidiocercariae of the *armatae* group and designated *Cercaria* type I.

Description: Body 228-276(254) long by 84-112(99) wide and covered with small spines that become less dense at the posterior end. Caudal pocket present. Tail 184-228(205) long by 29-35(32) wide at base. Oral sucker 53-63(58) long by 56-64(61) wide. Acetabulum 45-51(47) long by 44-53(50) wide. Stylet shouldered, 28-33(31) long. Five pairs of pre-acetabular penetration glands with ducts that empty near stylet. Ceca extend to post-acetabular level. Excretory bladder cellular and Y-shaped. Flame cell formula or number not determined.

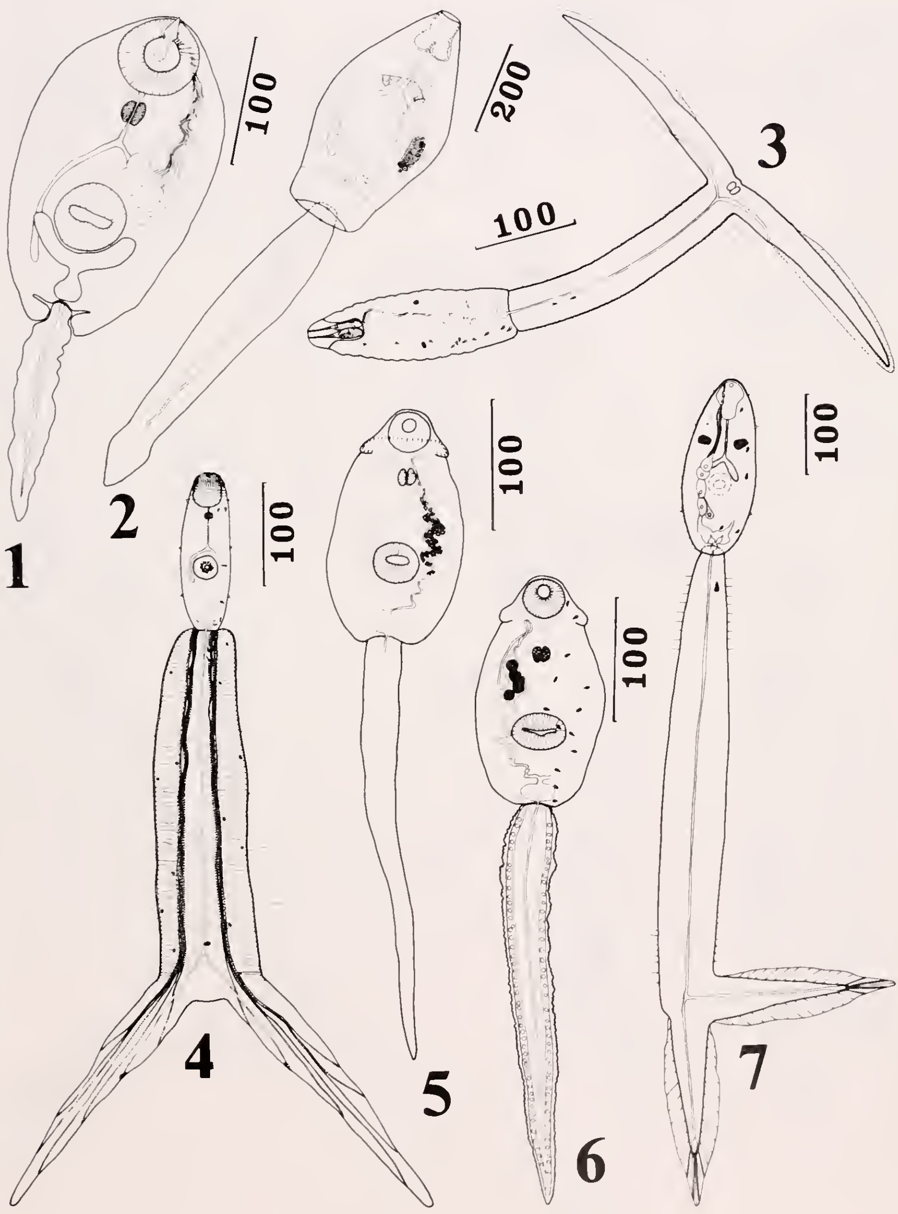
Ferrissia fragilis harboring these cercariae were collected only during July of the second summer and comprised 1% of the sampled population at BPB (Figure 21). Infection occurred in 0.8% of the sampled *F. fragilis* population during the same month at RAM (Figure 22). *Laevapex fuscus* from this locality, however, harbored infection throughout spring and summer. At SOR (Figure 23) *Cercaria* type I was present in *L. fuscus* almost year round with a peak seasonal incidence of 8.5% in August.

Cercaria Type II (Figures 2, 20, 21, 23, and 24)

Amphistome cercariae of the *diplocotylea* type, designated *Cercaria* type II, were found developing in both *Laevapex fuscus* and *Ferrissia fragilis* collected at SOR. *F. fragilis* from BHF, HIP, and BPB also harbored infections.

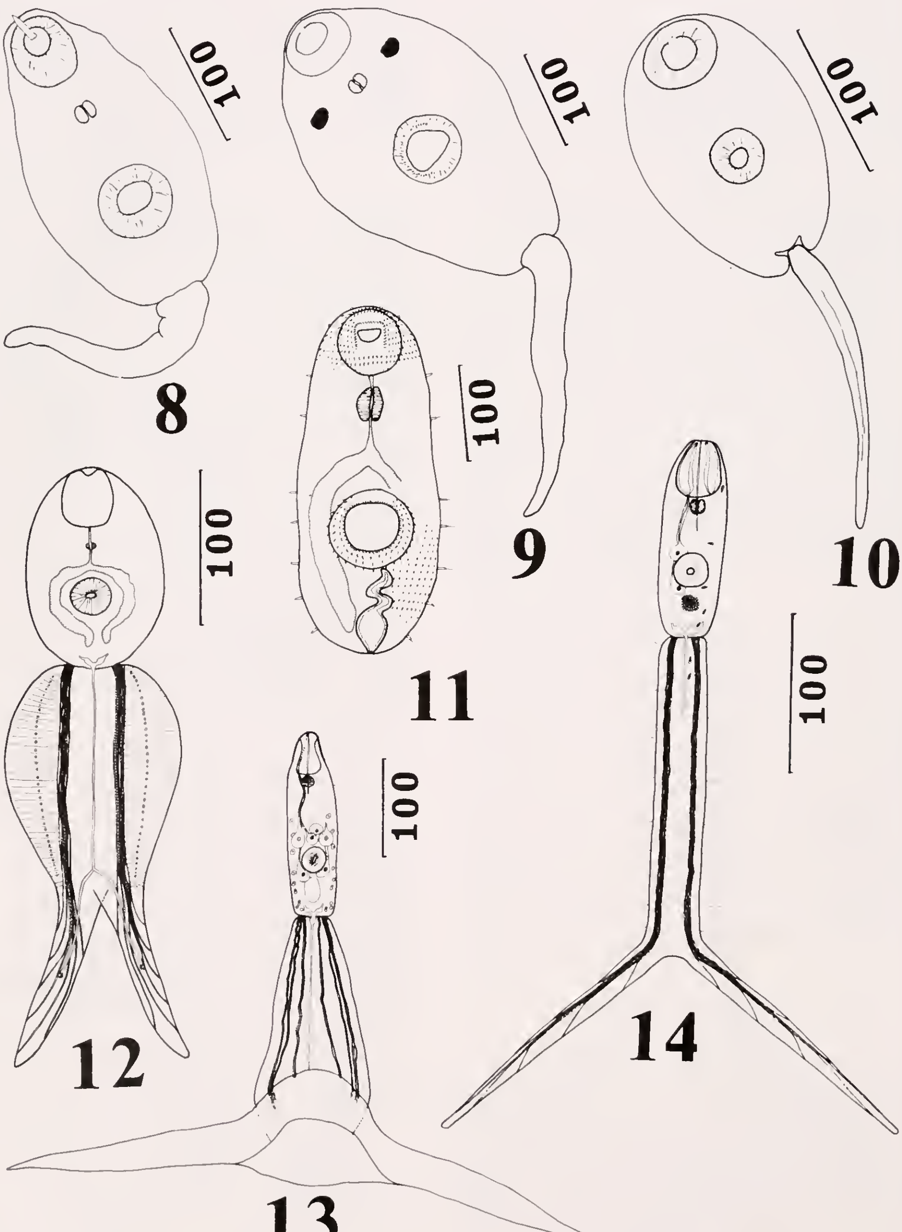
Description: Body 230-292(260) long by 102-144(123) wide. Tail 415-450(432) long by 35-46(40) wide. Oral sucker 118-

147(128) long. Acetabulum 40-77(57) long by 113-149(131) wide. Ceca thick walled, extend posteriorly to near level of excretory bladder. Paired excretory trunks containing many small concretions. Flame cell formula or number not determined.

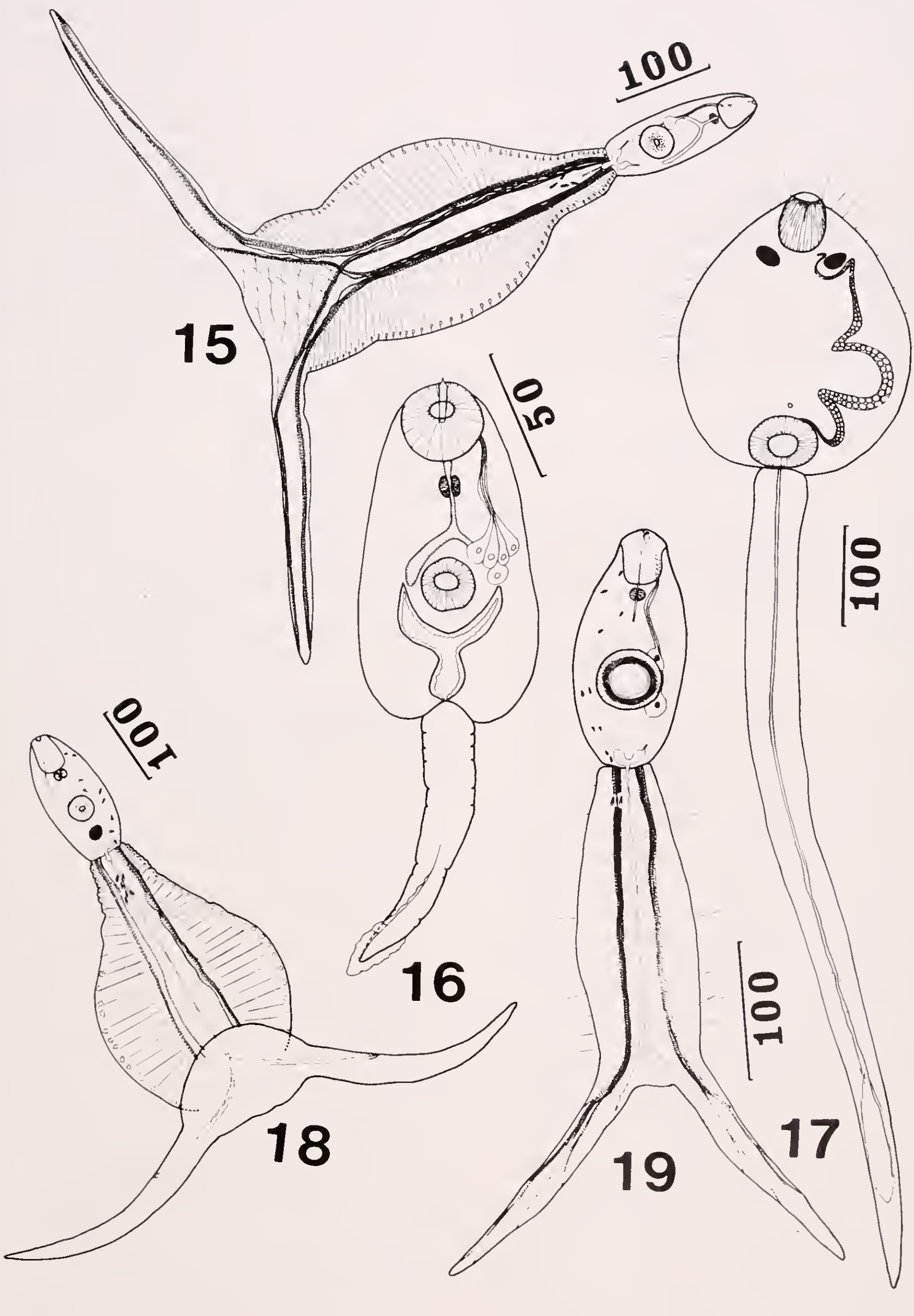


Figures 1-7. *Cercaria* types I-VII developing in southeastern Lousiana ancylid snails. Scale in microns.

Cercaria type II, although smaller, fits the description given by Krull and Price (1932) for the cercaria of *Megalodiscus temperatus*, and by Smith (1967) for larvae of that species developing in *Laevapex fuscus* and *Ferrissia fragilis* from Michigan. Smith reported an overall incidence of 14% for *F. fragilis*, whereas an inci-



Figures 8-14. *Cercaria* types VIII-XIV developing in southeastern Louisiana ancylids. Scale in microns.



Figures 15-19. *Cercaria* types XV-XIX developing in southeastern Louisiana ancylids. Scale in microns.

dence of only 1% was noted for infections in *L. fuscus*. Cercarial production in Michigan *F. fragilis* was in two distinct waves, one in spring and the other in autumn (Smith, 1967).

Like Smith, we noted a disparity in incidence of infection among the two limpet species. Of almost 5,000 *Laevapex fuscus* examined from SOR, only one harbored infection with *Megalodiscus temperatus*, while eight of 40 *Ferrissia fragilis* were infected. Two waves of cercarial production were observed. One began in late fall and continued until early spring, while the other began in early summer.

Cercaria Type III (Figures 3, 20, 22, 23, and 24)

Longifurcocercous, apharyngeate, monostome cercariae, with small eyespots, were found developing in all three limpet species and were collected at all localities except BPB.

Description: Body 179-207(194) long by 31-39(34) wide, with 12 annulations between oral sucker and acetabular anlagen. Two pairs of lateral setulae on posterior body near junction of tail stem. Tail stem 202-246(232) long by 26-37(31) wide, with five pairs of lateral setulae grouped near junction with body, and six or seven pairs grouped near bifurcation. Caudal bodies not observed in tail stem. Furcae 161-207(196) long by 16-23(17) wide, with delicate finfolds originating at level of excretory pores, which emptied on anterior surface of furcae. Oral sucker 37-55(46) long by 17-28(21) wide. Three pairs of penetration glands between eyespots and excretory bladder, with acetabular anlagen located immediately posterior to anterior pair. Genital primordium between posterior penetration glands and excretory bladder. Extent of ceca not determined. Eleven pairs of flame cells located in body and two pairs in tail.

Cercaria type III resembles the larva of *Posthodiplostomum minimum* (MacCallum, 1921), a parasite of the heron, *Nycticorax nycticorax* (Linnaeus, 1758). Two morphologically different cercariae have been described for *P. minimum*. Miller (1954) described *Cercaria minimum*, which bears similarity to *Cercaria* type III; however, Miller noted the presence of five pairs of caudal bodies in the tail stem, and 10 pairs of flame cells in the body and tail. *Cercaria minimum* Miller, 1954 developed in naturally infected *Physa heterostropha* Say, 1817 in Michigan. More recently, Bedinger and Meade (1967) reported on the life cycle of *Posthodiplostomum minimum*, the cercaria of which developed in naturally infected *Physa halei* Lea, 1864 in Texas. Those cercariae lack caudal bodies, have "flagellets" in two groups on the tail stem, and have 13 pairs of flame cells in the body and tail.

On morphological grounds *Cercaria* type III, although somewhat larger, more nearly resembles the cercaria described by Bedinger and Meade; however, in size, it resembles *Cercaria minimum*.

Cercaria Type IV (Figures 4, 20, 21, 22, 23, and 24)

Longifurcocercous, pharyngeate, distome cercariae were found developing in all three species of limpets and were collected at all five localities.

Description: Body 119-178(151) long by 41-62(51) wide, with anteriorly directed needle-like spines extending posteriorly to level of pharynx, and with three pairs of lateral papillate setulae. Tail stem 228-364(316) long by 72-98(77) wide, with four pairs of lateral setulae. Furcae 180-292 (239) long by 32-48(39) wide, with excretory pores opening at mid-length of posterior surface. Oral sucker 35-44 (39) long by 25-32(28) wide. Pharynx 9-12(10) long by 22-28(26) wide, with a single circle of inwardly directed, needle-like spines. Number and arrangement of penetration glands not determined. Ceca extended to postacetabular level. Six pairs of flame cells in body and two pairs in tail.

Cercaria Type V (Figures 5 and 20)

An echinostome cercaria, with spiny collar, was found developing only in *Hebetancylus excentricus* from BHF. Measurements of *Cercaria* type V used in the following description were taken from a single live specimen.

Description: Body 176 long by 148 wide, with an undetermined number of small collar spines. Tail without finfold, 392 long. Oral sucker 44 long by 44 wide. Acetabulum 50 long by 50 wide. Extent of ceca not determined. Many small concentrations restricted to middle and anterior portion of paired excretory trunks. Flame cell formula or number not determined.

Cercaria type V was collected only during June of the first summer and comprised 4.1% of the sampled *Hebetancylus excentricus* population (Figure 20).

Cercaria Type VI (Figures 6, 20, 21, 22, and 23)

Echinostome cercariae, without spiny collars, were found developing in all three limpet species at all localities except HIP.

Description: Body 168-196(184) long by 86-116(102) wide. Tail without finfold, 364-416(393) long by 43-53(46) wide, with pair of short flagellets near tip. Oral sucker 35-43(39) long by 38-43(40) wide. Acetabulum 37-50(43) long by 51-58(54) wide. Extent of ceca not determined. Paired excretory trunks each contain three or four large concentric concretions restricted to pre-acetabular region. Thirteen pairs of flame cells present in body.

Cercaria type VI may be a species of *Echinochasmus* Dietz, 1909, since cercariae of this genus often lack collar spines, have few and large excretory concentrations, and have short flagellets on the tail (Yamaguti, 1975).

Cercaria Type VII (Figures 7, 20, 21, and 22)

A brevifurcocercous, apharyngeate, distome cercaria of the turtle blood fluke family Spirorchiidae Stunkard, 1921 was found developing only in *Ferrissia fragilis* from BHF, BPB, and RAM.

Description: Body 192-256(219) long by 58-72(64) wide at acetabulum, with three pairs of lateral setulae. Anterior third of oral sucker covered with dense, fine spines. Spines around acetabulum large and numerous. Remainder of body covered with minute, sparse spines. Tail stem attached subterminally, 568-680(590) long by 52-67(60) wide. Short lateral setulae on tail stem arranged in two groups of nine pairs each. Anterior group all nonpapillate. Posterior group with last three pairs papillate. Furcae 200-268(227) long, with finfolds along margin. Oral sucker 44-69(60) long by 28-37(34) wide. Acetabulum protrusible, 24-30(28) long by 26-32(28) wide. Eyespots in second quarter of body. Five pairs of penetration glands from posterior margin of eyespots to fourth quarter of body. Sixth pair of fused glands in fourth quarter. Ceca extend to level of acetabulum. Five pairs of flame cells in body and one pair of large flame cells in tail. Under laboratory conditions cercariae emerged mostly at night. Life cycle studies (Turner and Corkum, 1977) indicated *Cercaria* type VII to be the larva of *Spirorchis scripta*.

Cercaria Type VIII (Figures 8 and 22)

A xiphidiocercaria of the *armatae* group parasitized only *Ferrissia fragilis* from RAM. Measurements from the following description were taken from a single living specimen.

Description: Body 252 long by 140 wide. Tail 203 long by 42 wide. Oral sucker 69 long by 64 wide. Stylet unshouldered, 25 long. Acetabulum 53 long by 64 wide. Extent of ceca not determined. Excretory bladder Y-shaped. Arrangement and number of flame cells or penetration glands not determined.

Cercaria Type IX (Figures 9 and 22)

An ophthalmoxiphidiocercaria of the family Allocreadiidae was found developing only in *Laevapex fuscus* collected at RAM. Measurements for the following description were taken from a single living specimen.

Description: Body 328 long by 228 wide at acetabulum. Tail 270 long by 43 wide. Oral sucker, with five rows of small, blunt spines forming a semicircle below mouth, 56 long by 69 wide. Acetabulum with two alternating circles of small, blunt spines, 64 in diameter. Stylet short and blunt. Eyespots in first quarter of body. Extent of ceca not determined. Number and arrangement of flame cells or penetration glands not determined.

According to Dr. Lewis E. Peters (1975, pers. comm.), *Cercaria* type IX appears "very similar to the cercaria that [he and Dr. J. Teague Self] studied in Oklahoma in the early 1960's." Peters also noted that he and Dr. Raymond Cable had confirmed identity of the cercaria, which also occurred in *Laevapex* from Indiana, to be that of *Allocreadium ictaluri*. Although Peters and Self (1963) reported *L. fuscus* as one of several second intermediate hosts, we were unable to find any harboring allocreadiid metacercariae among the 3,663 *L. fuscus* examined from RAM.

Cercaria Type X (Figures 10 and 23)

A small xiphidiocercaria of the *armatae* group, designated *Cercaria* type X, was found developing only in *Laevapex fuscus* at SOR.

Description: Body 152-182(169) long by 74-90(86) wide. Caudal pocket present. Tail 106-140(123) long by 30-37(35) wide. Acetabulum 24-28(26) long by 23-28(25) wide. Stylet slightly shouldered, 23-27(26) long. Extent of ceca not determined. Excretory bladder Y-shaped. Flame cell formula or number not determined. Penetration gland number and arrangement not determined. Pharynx, although present, was not observed.

Cercaria Type XI (Figures 11 and 22)

Tailless cercariae (cercariaea) of the family Lissorchiidae Poche, 1926 were found developing in *Laevapex fuscus* and *Ferrissia fragilis* at RAM.

Description: Body 324-392(358) long by 80-128(101) wide, with nine pairs of lateral papillate setulae. Pharynx 24-28(26) long by 26-31(29) wide. Oral sucker 50-64(54) long by 51-61(57) wide, with mouth surrounded on three sides by two alternating rows of small, inwardly directed spines. Acetabulum 58-69(63) long by 58-71(64) wide, with two alternating circles of small, inwardly directed spines surrounding inner rim, and a third row present on anterior quadrant of inner rim. Tegument with larger spines directed posteriorly; however, spines absent from area between oral sucker and acetabulum. Ceca extend to near base of excretory bladder. Excretory bladder cylindrical and thick walled. Flame cell and penetration gland number and arrangement not determined.

Cercaria type XI resembles *Cercariaeum* type I described by Duncan and DeGiusti (1976); however, it differs in host specificity (not restricted to *Laevapex fuscus*), in size (slightly larger than *Cercariaeum* type I), in arrangement of lateral papillate setulae, and in number and arrangement of small spines on the oral sucker and acetabulum.

Duncan and DeGiusti (1976) noted that papillae pattern and number were variable; however, tegumental spination pattern was fixed. Differences in size may be attributable to techniques used by these authors, since they first relaxed emergent cercariae in menthol solution prior to fixing in hot 10% formalin. They also measured cercariae in groups of twenty under a "floating" coverslip.

Cercaria Type XII (Figures 12 and 21)

A longifurcocercous, pharyngeate, distome cercaria was found developing only in *Hebetancylus excentricus* from BPB.

Description: Body 108-156(131) long by 62-99(83) wide. Tail stem 108-200(149) long by 83-150(108) wide. Furcae 104-163(124) long. Oral sucker 35-48(41) long by 29-39(34) wide. Acetabulum 23-29(25) long by 23-30(26) wide. Ceca surround acetabulum and extend to post-acetabular position. Tail, as seen in lateral view, appearing as a pair of empty, pressed trousers with excretory pores opening on inner surface of furcae. Number and arrangement of flame cells and penetration glands not determined.

Cercaria Type XIII (Figures 13, 20 and 24)

A longifurcocercous, pharyngeate, distome cercaria parasitized only *F. fragilis* from HIP and BHF.

Description: Body 164-220(193) long by 41-58(46) wide. Tail stem 288-316(297) long by 172-196(186) wide at bifurcation. Furcae 220-268(248) long by 40-60(48) wide. Oral sucker 44-58(51) long by 25-39(28) wide. Pharynx 12-14(13) long by 14-18(17) wide. Acetabulum with three circles of blunt, concentrically placed spines, 25-32(30) long by 30-35(32) wide. Three pairs of penetration glands, two pre- and one post-acetabular. Several smaller pairs of cells scattered throughout the body. Genital primordium between posterior penetration glands and excretory bladder. Extent of ceca not determined. Anterior body to level of pharynx covered with small, dense spines. Flame cell formula or number not determined. Tegument on tail stem at bifurcation formed into loose, bladder-like "skirt" continuous with furcae. "Skirt" most evident when cercariae were placed under coverslip pressure. Figure 13 was drawn without coverslip pressure and shows "skirt" in folded configuration.

Cercaria Type XIV (Figures 14 and 20)

A longifurcocercous, pharyngeate, distome cercaria was found developing only in *Ferrissia fragilis* from BHF.

Description: Body 112-153(127) long by 32-51(44) wide, with small dense spines to level of mid-oral sucker. Tail stem 187-220(207) long, with nine pairs of lateral setulae. Furcae 162-189(179) long by 14-18(16) wide. Oral sucker 32-41(37) long by 26-34(30) wide. Acetabulum 18-21(20) long by 19-25(23) wide, with two alternating circles of small, blunt spines. Two pairs of penetration glands, one pre-acetabular the other post-acetabular. Genital primordium between posterior pair and excretory bladder. Extent of ceca not determined. Five pairs of flame cells in body and two pairs in tail.

Cercaria Type XV (Figures 15 and 24)

A single *Ferrissia fragilis* collected at HIP was found to harbor infection with a longifurcocercous, pharyngeate, distome cercaria.

Description: Body 132-188(161) long by 34-52(41) wide, with small, dense spines to level of mid-oral sucker, less densely spined to level of gut bifurcation. Tail stem 280-336(305) long by 124-152(140) wide. Furcae 220-276(252) long by 28-46(35) wide. Oral sucker 35-52(45) long by 20-30(25) wide. Acetabulum 25-30(27) long by 28-32(30) wide, with three alternating circles of short, blunt spines. Ceca extend to mid-acetabulum. Two pairs of penetration glands, one pre- and the other post-acetabular. Muscle fibers from median portion of each fiber tract in tail stem contralateral in furca and form a chiasma anterior to bifurcation. Lateral fibers ipsilateral. Two pairs of flame cells in tail. Flame cell number or arrangement for body not determined.

Cercaria Type XVI (Figures 16 and 20)

A single *Ferrissia fragilis* collected at BHF was found to harbor infection with a small xiphidiocercaria of the *ornatae* group.

Description: Body 108-150(130) long by 58-72(64) wide. Tail with finfold, 90-122(108) long by 18-23(20) wide. Oral sucker 32-35(33) long by 30-35(32) wide. Acetabulum 18-23(21) long by 21-23(22) wide. Stylet shouldered 16-21(19) long. Five pairs of penetration glands and ceca extend to mid-acetabular level. Excretory bladder cellular and Y-shaped. Flame cell formula or number not determined.

Cercaria type XVI may be the larva of the frog lung fluke *Haemaetoloechus breviplexus*. In size of body and tail it appears intermediate between that noted by Schell (1965) for *H. breviplexus* larvae developing in experimentally infected *Gyraulus similaris* in Idaho, and that reported by Underwood and Dronen (1977) for those in an unknown species of experimentally infected *Ferrissia* from Texas. All other measurements, however, agree with those of Schell.

Cercaria Type XVII (Figures 17 and 21)

Heavily pigmented amphistome cercariae of the *pigmentata* group were found developing in *Ferrissia fragilis* from BPB, and *Laevapex fuscus* from RAM.

Description: Body 256-352(281) long by 160-273(233) wide, with 12 pairs of lateral setulae arranged along anterior half. Tail 506-800(702) long by 48-68(57) wide. Oral sucker 51-72(61) long by 48-69(54) wide. Acetabulum subterminal, 58-83(73) long by 62-101(85) wide. Eyespots large and oval, located in anterior quarter of body. Extent of ceca not determined. Paired excretory trunks filled with concretions and extending anteriorly with several coils until reaching level of oral sucker before turning posteriorly. Flame cell formula or number not determined. Cercariae maintained under laboratory conditions emerged only in morning, within five minutes after exposure to light, and quickly encysted on green vegetation.

Cercaria type XVII most nearly resembles the cercaria of *Stichorchis subtriquetrus* (Rudolphi, 1814), a cecal parasite of the beaver, *Castor canadensis* Kuhl, 1820. Bennett and Humes (1939) reported on the pre-cercarial development of this species in experimentally infected lymnaeid snails, *Lymnaea parva* Lea, 1841, in Louisiana. Bennett and Allison (1958) later obtained cercariae from experimentally infected *L. parva*; however, these authors suggested that this snail was not a satisfactory host because of high mortality among infected individuals.

Except for a slightly shorter tail, *Cercaria* type XVII fits the description for *S. subtriquetrus* given by Orloff (1941) for cercariae obtained from naturally infected *Planorbis vortex* (Linnaeus, 1758), *Lymnaea ovata* (Draparnaud, 1805), the operculate hydrobiid, *Bithynia tentaculata* (Linnaeus, 1758), and the terrestrial snail, *Succinea putris* (Linnaeus, 1758), in Russia.

Cercaria Type XVIII (Figures 18 and 24)

A single *Ferrissia fragilis* from HIP was found to harbor infection with a longifurcocercous, pharyngeate, distome cercaria.

Description: Body 150-184(166) long by 48-62(56) wide, with two pairs of lateral setulae, one pair near mouth and another papillate pair at level of excretory bladder. Anterior body to level of mid-oral sucker covered with small, dense spines. Tail stem 240-316(297) long by 128-172(160) wide, with two groups of lateral setulae, two pairs near junction with body and four pairs near bifurcation. Furcae 208-268(243) long, with excretory pores opening on anterior surface of mid-length. Oral sucker 40-44(42) long by 28-35(30) wide. Acetabulum 28-32(30) long by 30-35(33) wide, with several alternating circles of small, blunt concentrically placed spines. Extent of ceca not determined. Number and arrangement of penetration glands not determined; however, one pair pre-acetabular. Genital primordium between acetabulum and excretory bladder. Nine pairs of flame cells in body and three pairs in tail. Tegument on tail stem at bifurcation formed into loose, bladder-like "skirt" continuous with furcae.

Presence of three pairs of flame cells in the tail stem seems to be a deviation from a maximum of two pairs noted for other cercariae of this type (Yamaguti, 1975). Since only nine pairs were observed in the body, perhaps one pair in the tail may have originally been derived from the body complement.

Cercaria Type XIX (Figures 19 and 24)

A single *Ferrissia fragilis* from HIP was found to harbor infection with a longifurcocercous, pharyngeate, distome cercaria.

Description: Body 148-204(170) long by 56-96(76) wide. Tail stem 248-284(256) long by 80-101(90) wide, with 10 pairs of lateral setulae. Furcae 208-220(213) long by 22-32(27) wide, with excretory pores opening on posterior surface. Oral sucker

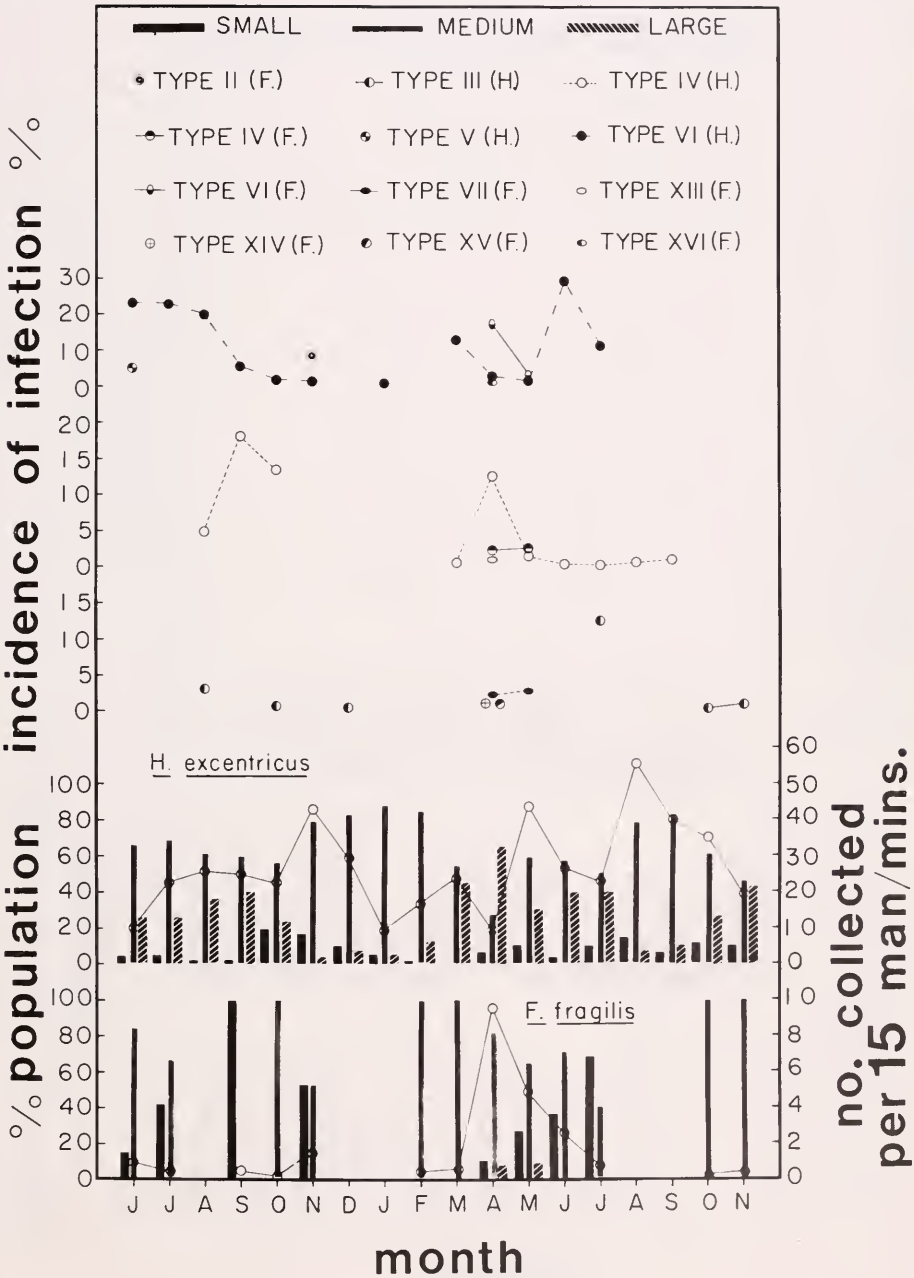


Figure 20. Monthly incidence of infection, population structure, and index of relative abundance for (H.) *Hebetancylus excentricus* and (F.) *Ferrissia fragilis* at Ben Hur Experimental Farm. Small, medium, and large refer to size classes of limpets. Cercarial type and limpet host combinations are indicated by various symbols. Relative abundance is indicated by circle with unbroken line.

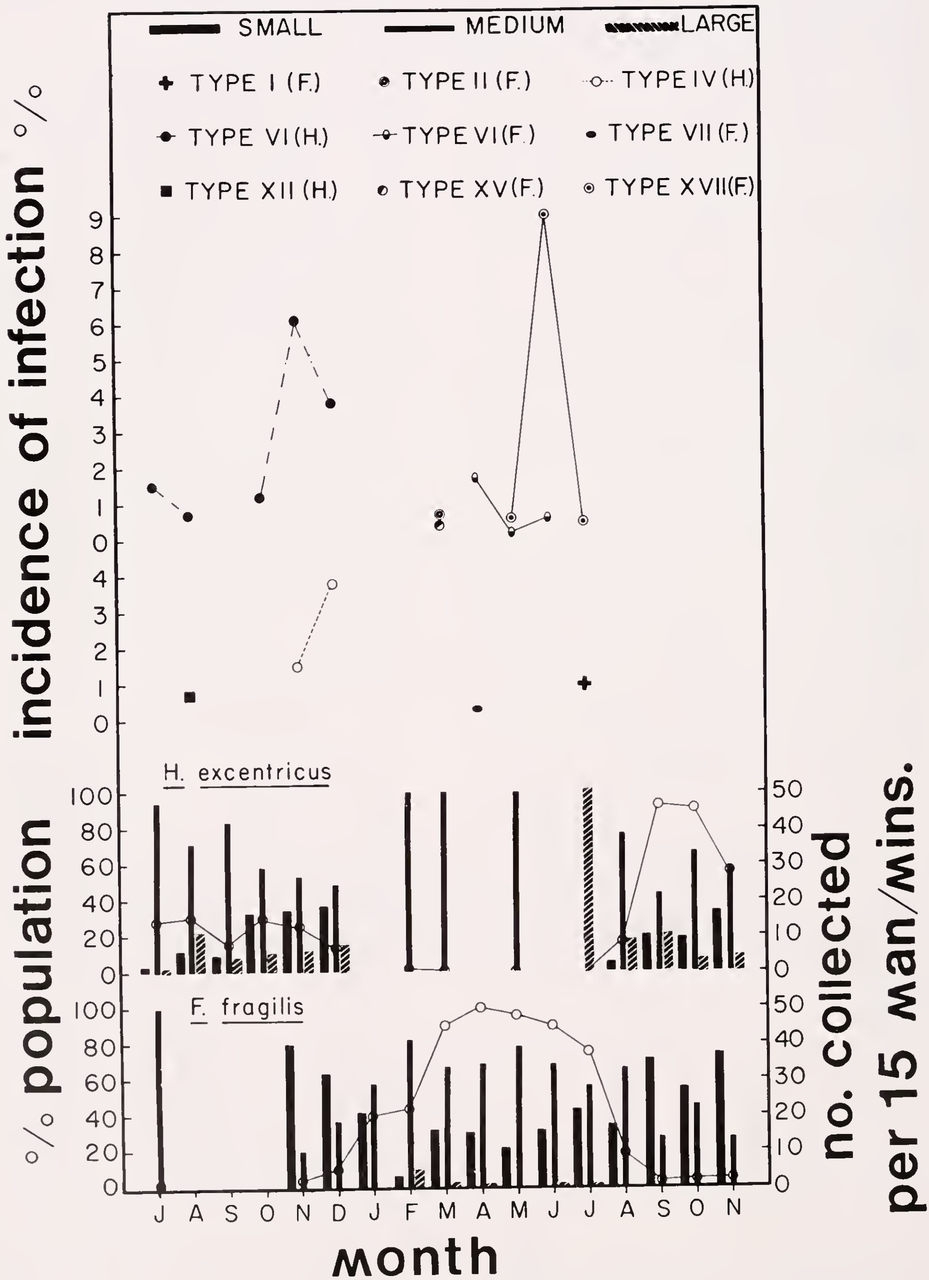


Figure 21. Monthly incidence of infection, population structure, and index of relative abundance for (H.) *Hebetancylus excentricus* and (F.) *Ferrissia fragilis* at Beaver Pond Branch.

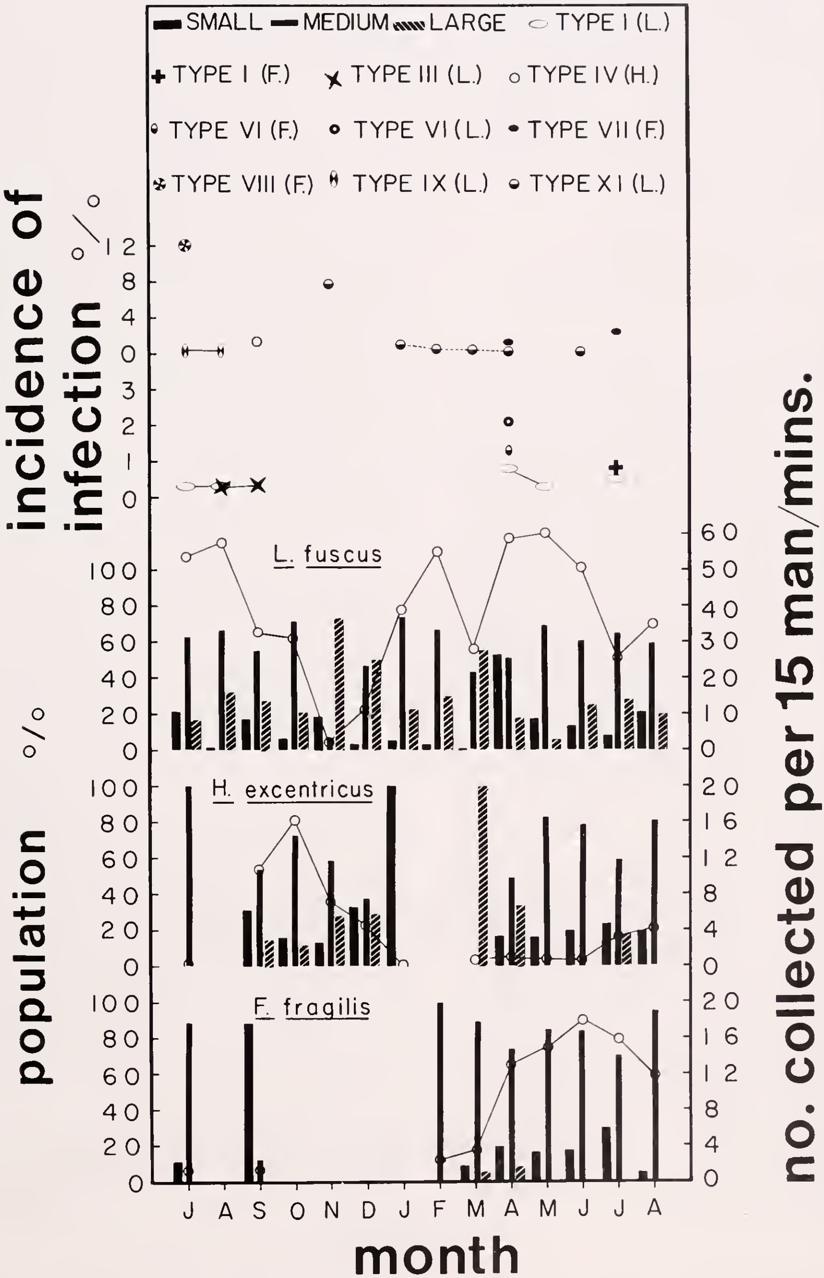


Figure 22. Monthly incidence of infection, population structure, and index of relative abundance for (L.) *Laevapex fuscus*, (H.) *Hebetancylus excentricus*, and (F.) *Ferrissia fragilis* at Ramah.

39-51(45) long by 30-39(35) wide. Pharynx 12-15(14) long by 14-17(16) wide. Acetabulum 48-57(52) long by 46-62(51) wide, with six circles of small, blunt spines around inner rim. Extent of ceca not determined. Two pairs of penetration glands, one pre- and the other post-acetabular. Ten pairs of flame cells in body and two pairs in tail.

DISCUSSION

Ecology of Southeastern Louisiana Ancylids

Although *Ferrissia fragilis* accounted for only 15% of the total ancylids collected and examined, it occurred at all sampled habitats. In contrast, *Laevapex fuscus*, which comprised 45% of the ancylids studied, was restricted to lentic habitats, and thus displayed greater ecological specialization. *Hebetancylus excentricus* was intermediate in ecological specificity because, although occurring at all habitats, it was not as successful, in terms of abundance, as *F. fragilis* at lotic BPB or *L. fuscus* at lentic SOR. McMahon (1976) stated this relationship when he noted, "representative species of these three limpet genera from the progressively less euryoecic series: *Ferrissia-Hebetancylus-Laevapex*."

Bivoltine and trivoltine reproductive patterns with overlapping generations, as exhibited by *Laevapex fuscus* and *Hebetancylus excentricus*, partially account for their predominance over *Ferrissia fragilis* at most habitats. Although McMahon (1976) noted a trivoltine pattern for a Texas *L. fuscus* population, we found no more than a bivoltine for southeastern Louisiana populations. Even at eutrophic SOR the reproduction-recruitment cycle occurred only twice during the 14-month survey.

Role of Southeastern Louisiana Ancylids in Trematode Ecology

Southeastern Louisiana ancylids play a major role in trematode life cycles because collectively they host at least 19 cercarial species, which in turn utilize five classes of vertebrates as definitive hosts.

Expectedly, the ecology of trematode intramolluscan stages was closely related to the ecology of the limpet hosts. Nowhere was this more evident than BHF (Figure 20), where the bivoltine reproduction of *Hebetancylus excentricus* was reflected in two cycles of cercarial production. The winter discontinuity in cercarial production reflected an interim between limpet cycles. Seasonality of those cercariae developing in *Ferrissia fragilis* did not demonstrate biannual patterns. Rather, individual trematode species were seasonal with discrete annual periods of cercarial production.

At BPB (Figure 21) the annual generation of each limpet species is reflected in an annual generation of cercaria production. *Cercaria* type XVII (probably *Stichorchis subtriquetrus*) from this locality demonstrated a pronounced seasonality, which must also relate to the life history of the beaver. Lowery (1974) noted that, although little is known about reproduction in Louisiana beaver, young are thought to be born in April or May. If true, June cercarial emergence and encystment on aquatic vegetation may be correlated with feeding habits of recently weaned beaver, and thereby insured infection of a presumably more susceptible individual.

A similar seasonal correlation between cercarial emergence and life history of definitive host may exist for *Cercaria* type VII (*Spirorchis scripta*) and the turtle, *Chrysemys scripta* (Schoepff, 1793). Cagle (1950) reported egg hatching in Louisiana *C. scripta* to occur from early July to early September. Peak cercarial emergence in July probably insures infection of young, susceptible individuals, not previously exposed or harboring a current infection with this blood fluke.

Differences in population biology of *Laevapex fuscus* at RAM and SOR were earlier attributed to putative differences in primary productivity between these habitats. As shown in Figures 22 and 23, these differences are in turn reflected in

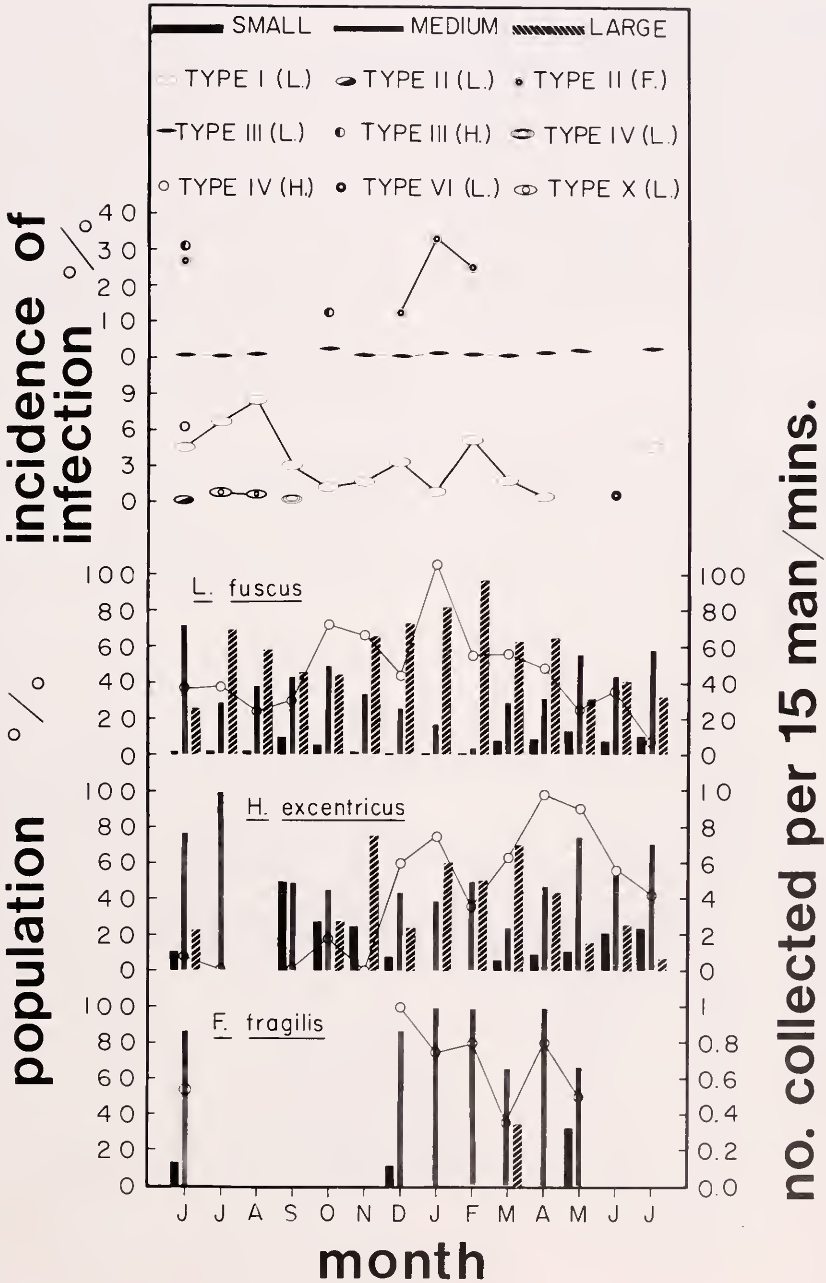


Figure 23. Monthly incidence of infection, population structure, and index of relative abundance for (L.) *Laevapex fuscus*, (H.) *Hebetancylus excentricus* and (F.) *Ferrissia fragilis* at Sorrento.

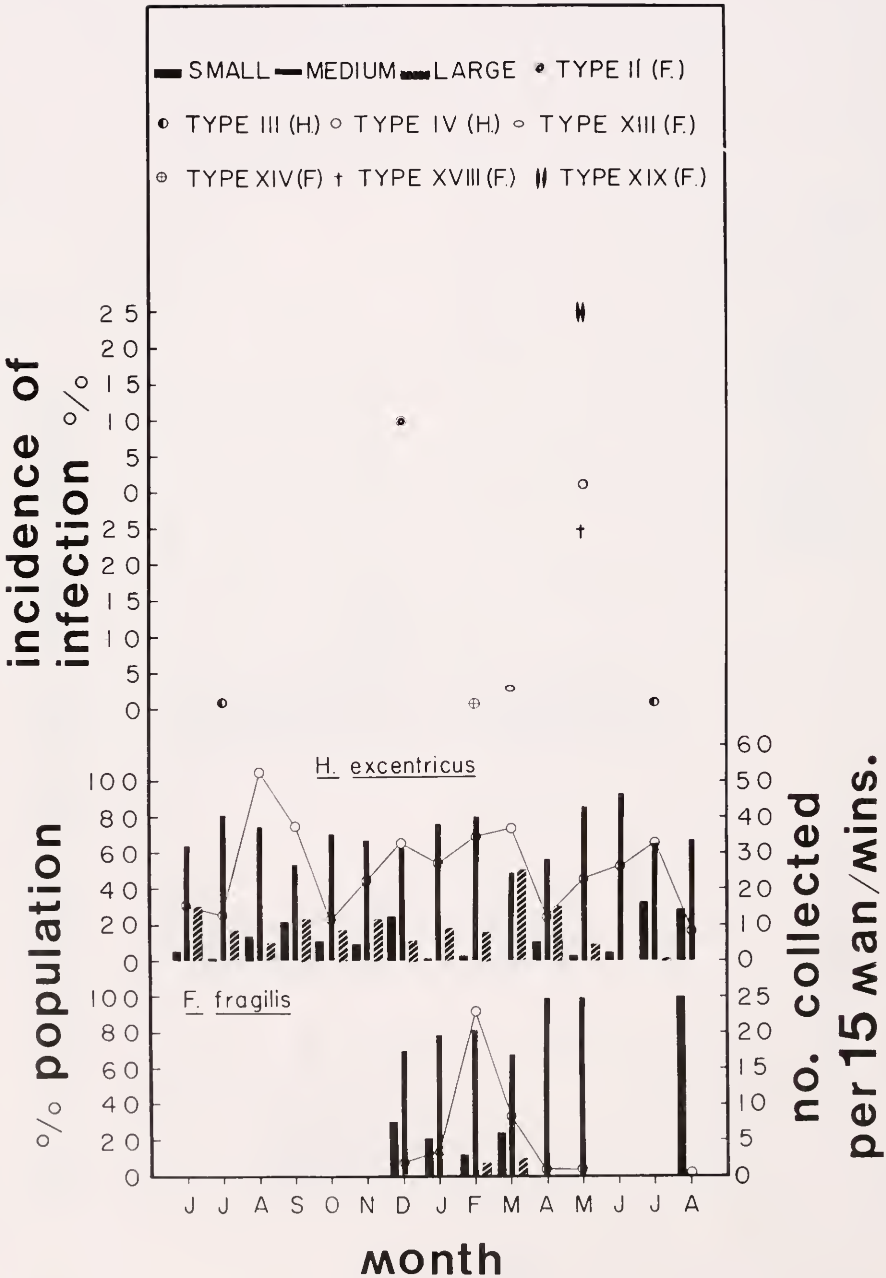


Figure 24. Monthly incidence of infection, population structure, and index of relative abundance for (H.) *Hebetancylus excentricus* and (F.) *Ferrissia fragilis* at Head of Island Pond.

the ecology of the respective trematode faunas. Seasonality of infection in *L. fuscus* at RAM was indicative of a single, annual host generation; however, two cercarial species were maintained essentially year round in SOR *L. fuscus*, and thus reflected relative stability in the *L. fuscus* population.

Head of Island Pond (Figure 24) was productive enough to permit a trivoltine pattern for *Hebetancylus excentricus*, but was faunistically poor in digenetic trematodes hosted by ancylids. Only seven host-parasite combinations were observed, as compared to 12 at BHF. Five of the seven involved the single generation of *Ferrissia fragilis*.

Differences in species composition of those trematode faunas hosted by ancylids can be explained on the basis of ecological differences in the habitats, i.e. absence or presence of suitable definitive or other hosts.

Phylogeny of Southeastern Louisiana Ancylids

Basch (1963) noted a general similarity in radular patterns among *Ferrissia, Laevapex,* and *Hebetancylus*. He also compared anatomy of certain "soft-parts" and noted a similar verge for *Hebetancylus* and *Ferrissia*; however, the *Hebetancylus* pseudobranch was bilobed like *Laevapex*. Basch thus proposed that *Hebetancylus* had greater affinity with *Laevapex*, which *he believed to be more advanced. Hebetancylus* and *Ferrissia* were suggested to have evolved independently from a common ancestor that was in turn derived from the family Planorbidae. However, Turner (1978) reported that *Hebetancylus*, like *Ferrissia*, formed a septum or horizontal calcareous shelf partially closing the shell aperture. This shell-like epiphragm, which was deposited by the posterior margin of the mantle, has not been reported for *Laevapex*. Because of this observation we believe that *Hebetancylus* and *Ferrissia* did not evolve independently and that *Hebetancylus* occupies an intermediate phylogenetic position between *Ferrissia* and *Laevapex*.

Digenetic trematodes generally exhibit greater host specificity for their molluscan first intermediate host than for subsequent hosts, perhaps because of a longer host-parasite evolutionary association (Pearson, 1972). In light of this generalization, we compared the trematode faunas hosted by each southeastern Louisiana ancylid species. Similarities and differences between respective faunas should reflect the emended phylogeny we have proposed.

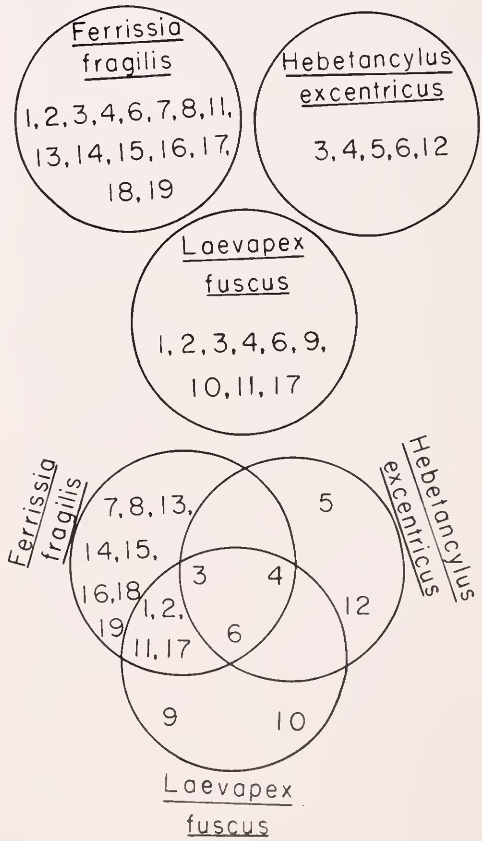


Figure 25. Southeastern Louisiana ancylid species as circles encompassing hosted cercariae and as overlapping circles encompassing "shared" and exclusively hosted cercariae.

Figure 25 depicts each of the three species as a circle encompassing hosted cercariae, which for convenience have been assigned arabic rather than conventional roman numeral designations. Figure 25 also demonstrates overlap or "sharing" of cercarial species.

Only an echinostome (type VI), a longifurcocercous distome (type IV), and *Cercaria* type III, tentatively identified as *Posthodiplostomum minimum*, were "shared" by all three limpet species. None were "shared" jointly by *Hebetancylus* and *Laevapex*, or by *Hebetancylus* and *Ferrissia*. *Ferrissia* and *Laevapex* jointly "shared" xiphidiocercaria (type I), *Megalodiscus temperatus* (type II), *Lissorchis* sp. (type XI), and *Stichorchis subtriquetrus* (type XVII).

Ferrissia seems to be the least specialized. Even though sympatric with the other genera, *Ferrissia* maintained the ability to host exclusively four times as many cercariae. This fact becomes more significant when noted that *F. fragilis* comprised only 15% of all limpets examined. Relative nearness of *Ferrissia* to the planorbid ancestral stock is suggested because at least five cercariae, hosted exclusively by *F. fragilis* or "shared" jointly with *Laevapex fuscus*, are also hosted by planorbids.

The relative positions of *Laevapex* and *Hebetancylus* are less clear. *Laevapex* and *Ferrissia* have more cercariae in common than *Hebetancylus* and *Ferrissia*; however, one cercaria (type XVII) is so broad in host specificity as to develop in prosobranch and both orders of pulmonate gastropods. Furthermore, on the basis of our study, and that of Smith (1967), *L. fuscus* does not appear to be as suitable host for *Megalodiscus temperatus* as does *F. fragilis*.

Laevapex fuscus and *Ferrissia fragilis* are widely distributed throughout the U.S. east of the Rocky Mountains (Basch, 1963; Clarke, 1973). Thus, the explanation for this "sharing" of cercariae by southeastern Louisiana *Laevapex* and *Ferrissia* may be found in the long sympatric association of these limpets in North America. Whereas, *Hebetancylus excentricus* is Caribbean in distribution with its historical, ecological associations in Central and South America, *H. excentricus* has been reported in North America from southern Florida, coastal Georgia (Basch, 1963), south central Texas (Pilsbry, 1889; Walker, 1903), north central Texas (McMahon and Aldridge, 1976), southern Oklahoma (McMahon, *et al.*, 1976), and southeastern Louisiana (Turner, 1978).

Finally, the fact that *Laevapex* hosts an allocreadiid (type IX), all others of which are hosted by sphaeriid clams, would tend to separate it from other ancylids and supports its placement in a highly derived phylogenetic position.

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